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Effect of river size on Amazonian primate community structure: A biogeographic analysis using updated taxonomic assessments

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Abstract

The mechanisms that underlie the diversification of Neotropical primates remain contested. One mechanism that has found support is the riverine barrier hypothesis (RBH), which postulates that large rivers impede gene flow between populations on opposite riverbanks and promote allopatric speciation. Ayres and Clutton-Brock (1992) demonstrated that larger Amazonian rivers acted as barriers, delineating the distribution limits of primate species. However, profound changes in taxonomy and species concepts have led to the proliferation of Neotropical primate taxa, which may have reduced support for their results. Using the most recent taxonomic assessments and distribution maps, we tested the effect of increasing river size on the similarity of opposite riverbank primate communities in the Amazon. First, we conducted a literature review of primate taxonomy and developed a comprehensive spatial database, then applied geographical information system to query mapped primate ranges against the riverine geography of the Amazon watershed to produce a similarity index for opposite riverbank communities. Finally, we ran models to test how measures of river size predicted levels of similarity. We found that, almost without exception, similarity scores were lower than scores from Ayres and Clutton-Brock (1992) for the same rivers. Our model showed a significant negative relationship between streamflow and similarity in all tests, and found river width significant for the segmented Amazon, but not for multiple Amazon watershed rivers. Our results support the RBH insofar as they provide evidence for the prediction that rivers with higher streamflow act as more substantial barriers to dispersal, and accordingly exhibit greater variation in community composition between riverbanks.

KEYWORDS

distributions, diversification, riverine barrier hypothesis, similarity index

1 | INTRODUCTION

Numerous hypotheses have been proposed to account for Neotropical diversification, but which environmental feature was the vicariant agent that caused populations to become separated and subsequently genetically differentiated remains disputed (Colwell, 2000). The riverine barrier hypothesis (RBH) was the earliest hypothesis of a biogeographical mechanism for species diversification in the Amazon. It stemmed from observations that range boundaries of primates, birds, and insects often abut at rivers (Wallace, 1854). It was more recently supported in a seminal study by Ayres and Clutton-Brock (1992) that provided evidence for the prediction that river systems act

as barriers which delineate species ranges, dividing populations, and causing isolation. However, recent, profound changes in taxonomy and species concepts has resulted in major revisions to Neotropical primate taxonomy which could invalidate the results of this study and reduce support for the RBH. Based on the latest species revisions and distribution data, this study aims to examine whether one of the key predictions of the RBH still holds for Neotropical primates.

The RBH postulates that rivers and river systems can act as barriers to the dispersion of species, dividing populations, and causing isolation. Competing with the RBH is the Pleistocene refugium hypothesis, a model of allopatric speciation that originally received wide support, which posits that during ice age glacial maxima previously connected populations became separated, persisting in pockets of forest isolated from each other, providing a vicariant mechanism for speciation (Haffer, 1969; Rull, 2011). There are further vicariance-based diversification models, such as the Miocene marine incursion, structural arches, and disturbance vicariance (Aleixo, 2004; Kay, 2015; Leite & Rogers, 2013). These different proposed mechanisms for diversification are not necessarily mutually exclusive. The vicariant agents discussed above are estimated to have occurred at different points in geological time meaning they could be complimentary. Previously, mainly biogeographical and paleoecological approaches were only available to draw conclusions about the origins of diversity and distributions. Based on this type of evidence, acceptance of the Pleistocene refugium hypothesis was promoted. However, molecular phylogenetic methods have not generally bolstered validity for Quaternary diversification, instead pointing toward a model involving a Tertiary (mainly Neogene) origin for Neotropical species, which does provide support for the RBH (Rull, 2011).

Recent fossil discoveries suggest that primates first colonized the Neotropics in the late Eocene or early Oligocene between ~35 and 40 Mya (Bond et al., 2015; Defler, 2019; Fleagle, 2018; Poux, Chevret, Huchon, de Jong, & Douzery, 2006), before the final uplift of the Andes and subsequent reorganization of the Amazonian drainage system (Hoorn, Wesselingh, ter Steege, Bermudez, & Mora, 2010; Latrubesse et al., 2010). Platyrrhine taxa rapidly diversified, forming many now-extinct taxa, with the extant platyrrhine genera beginning to appear in the early and middle Miocene (Kay, 2015; Marivaux et al., 2016). The present Neotropical region, and particularly the Amazon, harbors a species diversity vastly disproportionate to its geographic area. According to the IUCN/SSC Primate Specialist Group, there are 216 platyrrhine taxa. Molecular data from several systematics studies have converged on the genus-level phylogeny of extant platyrrhines. There are three monophyletic clades within the platyrrhines: cebids, atelids, and pitheciids (Kay, 2015; Opazo, Wildman, Prychitko, Johnson, & Goodman, 2006; Wildman, Jameson, Opazo, & Yi, 2009). However, taxonomic inflation from taxonomic revisions, rather than discovery of new species in situ, has led to substantial increases in the number of recognized species (Groves, 2014; Isaac & Purvis, 2004; Zachos et al., 2013), in large part due to a shift toward the phylogenetic species concept (PSC; Agapow et al., 2004; Frankham et al., 2012; Hausdorf, 2011). It should be recognized that the details of platyrrhine taxonomy are widely disputed (Groves, 2001b; Rylands & Mittermeier, 2009; Rylands, Mittermeier, & Silva, 2012), presenting a challenge to researchers seeking to decipher the history of species diversity (Moritz, Patton, Schneider, & Smith, 2000; Opazo et al., 2006; Schneider & Sampaio, 2015).

Studies across a range of taxonomic groups have demonstrated the inhibiting effect of rivers by showing how species assemblages vary on opposite riverbanks and by investigating the historical evolutionary relationships between them (Boubli et al., 2015; Leite & Rogers, 2013; Lynch Alfaro, Boubli, et al., 2015; Ribas, Aleixo, Nogueira Afonso, Miyaki, & Cracraft, 2012). The RBH makes several predictions which are often a focus of research. Specifically, the following predictions would support river formation as the primary driver of primate speciation: (a) reciprocally monophyletic taxa should exist on opposite riverbanks; (b) sister taxa should exist on opposite riverbanks. Nonsister relationships suggest the river could be a meeting point for taxa that diverged elsewhere, and is only a dispersal barrier; (c) similarity in species composition on opposing banks should be highest where the barrier effect is reduced; (d) similarity in species composition on opposite banks should be higher for species that can colonize várzea forest, than for species restricted to terra firma forest; (e) divergence times for all taxa on opposite banks should be similar, particularly in groups with similar characteristics; (f) lineage divergence times should be congruent with estimated river formation times.

The seminal study by Ayres and Clutton-Brock (1992) provided compelling evidence for prediction "(c)," showing that opposite-bank similarity of primate assemblages declines significantly (and independently) with both increasing width and increasing annual discharge. Furthermore, they suggest similarity shows a secondary increase at the river mouth where sediment deposition produces islands that increase permeability. To address major changes in taxonomy and species concepts, recent revisions to Neotropical primate taxonomy and associated changes in species distributions, we repeat, and expand the scope of the classic biogeographic study of Ayres and Clutton-Brock (1992) to re-evaluate the effect of measures of river size on the actual distribution of Amazonian primate species.

2 | METHODS

2.1 | Study area

The Amazon drainage basin is a major component of the Neotropical region, comprising mostly lowland rainforest habitats. It extends across South America from the eastern Andean slopes to the Atlantic

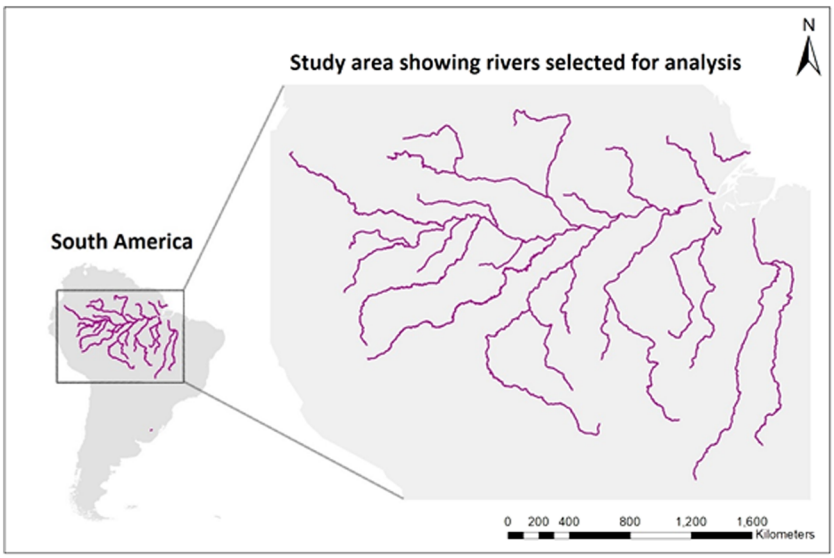

FIGURE 1 Map of South America showing Amazon basin watershed and rivers selected for analysis. *Source:* Natural Earth Data

coast and across the Brazilian and Guiana Shield, covering an area over 8 million km^2 (Sioli 1984). We selected 25 rivers for analysis, 15 being the same as analyzed by Ayres and Clutton-Brock (1992), and 10 additional rivers from the same watershed (Figure 1 and Table 1).

2.2 | Database development

To investigate primate community make-up along Amazonian riverbanks we conducted a major literature review into the current state of platyrrhine taxonomy. For this study, we followed the classifications of Groves (2001b; 2005) and Wilson, Mittermeier, Ruff, Martinez-Vilalta, and Llobet (2013) as recommended by the IUCN/SSC Primate Specialist Group. When there was disagreement over the classification of a species or substantial taxonomic changes had occurred since publication, primary literature was used to include or exclude a given taxon. Data on the distributions of Neotropical primates were obtained from the Terrestrial Mammals Digital Distribution Maps of the IUCN Red List of Threatened Species Assessments 2008/2016 (IUCN, 2016) and the online database of "All the World's Primates" (Rowe & Myers, 2016). These distribution maps were compiled by specialists based on published records and firsthand specialist knowledge of the species and areas involved and represent the most up-to-date data set available. Shapefiles were imported into ArcMap 10.3.1 (ESRI, 2018) for exploration and comparison. All spatial records were screened and quality checked before inclusion. Taxonomic refinement has led to multiple identities for some taxa. The scientific name of each species was investigated to ascertain whether it was simply a duplicate masked by a synonym. Due to disagreement between authors on subspecies we only included full species in analyses. We checked the distribution of all species by visual comparison to estimated primate distributions in Wilson et al. (2013).

2.3 | Geographical information system (GIS) model

Analyses were made using ArcGIS 10.3.1 (ESRI, 2018). Initial maps of species distributions indicated that distributions were generally spatially distributed within interfluvial areas, and clearly abutted by certain rivers. Despite distribution polygons in the model broadly following river lines, most distributions did not align perfectly with rivers, and we suspected many of these overlaps to be an error, rather than true representations of primate ranges. We measured overlap areas, and a limit of 20,000 km^2 was employed, so that any area smaller than this was discounted. We made an effort to verify that these minor "bleeds" across interfluves were erroneous spatial data, and not representative of real-world primate ranges by checking them against published data on location records (Mittermeier, Rylands, & Wilson, 2013). It is possible that some species which do have naturally occurring distributions on opposite riverbanks were not included in our analyses. However, we assume that any such distribution could either represent recent colonization events and/or remnant historical populations and as we were looking at the broad-scale effects of rivers on distributions, these possibly marginal populations do not invalidate results, as even the largest barrier will always be permeable to some extent. Distributions that crossed rivers at headwaters were not considered error, as headwaters are characteristically narrow with lower streamflow and pose less of a barrier to primates than river sections further downstream (Ayres & Clutton-Brock, 1992). To avoid headwater permeability influencing results, distributions that appeared to have colonized the adjoining interfluve across the headwater only (defined as the first

TABLE 1 Showing information for rivers selected for analysis in this study

River names	Annual streamflow (m^3/s)	River width (km)	River length (km)	Rivers also analyzed by Ayres and Clutton-Brock (1992)	Water type
Amazon	103,192	3.5	6,427		Whitewater
Amapri	355	0.3	422		Clearwater
Aripuanã	6,195	0.1	870	Yes	Clearwater
Coari	540	0.8	530	Yes	Blackwater
Putumayo	45,992	0.2	1,610	Yes	Whitewater
Javari	3,175	0.4	1,050	Yes	Whitewater
Jari	1,067	0.7	790	Yes	Clearwater
Japurá	13,988	0.3	2,820	Yes	Whitewater
Juruá	1,952	0.3	3,100	Yes	Whitewater
Jutaí	2,105	1.4	1,050	Yes	Blackwater
Madeira	22,425	1.8	3,380	Yes	Whitewater
Negro	9,437	0.7	2,250	Yes	Blackwater
Purus	3,746	0.3	2,960	Yes	Whitewater
Trombetas	1,721	1.3	760	Yes	Blackwater
Tocatins	5,131	3	2,450	Yes	Clearwater
Tapajós	10,517	2	1,930		Clearwater
Xingu	5,873	2	1,640	Yes	Clearwater
Araguaia	2,090	1.4	1,910		Clearwater
Branco	2,959	0.6	560		Clearwater
Guaporé	752	0.8	1,210		Clearwater
Iriri	1,941	0.4	1,100		Clearwater
Jamanxim	904	0.5	510		Clearwater
Jiparaná	792	0.4	820		Clearwater
Nhamundá	518	1	470		Clearwater
Uaupés	2,588	0.5	1,050		Blackwater

20% of river length) were discounted. As with possible overlap of distributions in distribution maps, this could have led to the exclusion of some true overlap, but should not affect large scale trends.

2.4 | Similarity index

We calculated a similarity index using our GIS model (Fewster & Buckland, 2001) for opposite-bank primate communities of the 25 rivers. We measured similarity as ([% species on side A common to side B] + [% species on side B common to side A])/2, as per Ayres and Clutton-Brock (1992). In addition to our analysis of similarity between riverbanks for multiple rivers of varying size, we tested how similarity changed between the headwater and the mouth of the Amazon River. To do this we divided the Amazon River into 10 equal segments of 312 km and calculated similarity indices for each segment.

2.5 | Measures of river size

We measured the average streamflow of rivers as the mean of all streamflow data points for a given river and minimum streamflow was taken as the mean of all the lowest values recorded by streamflow-monitoring stations for a given river (GRDC, Germany). River width, measured at the midpoint of each river during the dry season, was adapted from Ayres and Clutton-Brock (1992). For additional rivers, we measured the width at the midpoint of each river using Google Earth satellite imagery (LandSat/Copernicus) from the dry season. In our analysis of the segmented Amazon River, we

plotted all available streamflow data for the Amazon River against distance from the headwater and used the trendline to interpolate streamflow values for each segment. Width for each segment was obtained by taking the average of 10 within-segment measurements, using satellite imagery from the dry season.

2.6 | Influence of watershed geology

Shifting river courses may have resulted in occasional passive transfer of primates, and this lateral channel migration is expected to be more common for rivers flowing through the Solimoes sedimentary basin than those running through the Brazilian and Guiana Shields so we also compare similarity across rivers for these three distinct watersheds.

2.7 | Statistical analysis

We used R statistical software, version 3.3.2 (R Core Team, 2014), for all statistical analyses. We tested data for normality with Shapiro–Wilk and Spearman's rank correlation tests for multicollinearity. We used generalized linear models (GLMs) to examine the "opposite-bank similarity response variable" as a function of explanatory variables, streamflow, and river width, with a binomial distribution of errors and the logit link function (Warton & Hui, 2011). All model variations were compared using the Akaike information criterion (AIC) and goodness of fit assessed by visual inspection of residual plots to detect violations of homogeneity of variance, normality of residuals, and independence of both explanatory variables and residuals. We chose the model with the lowest AIC score as the best description of the observed data. Finally, we also compared species similarity across rivers for distinct watersheds using a binomial logit GLM to determine whether geology might play a part in the strength of riverine barriers.

3 | RESULTS

3.1 | Spatial database for Neotropical primates

Data screening began with 421 spatial records from three different data sets (Figure S1). We identified and removed 155 duplicates, 113 synonym name duplicates, 83 subspecies and 2 erroneous records to generate a database containing 168 shapefiles suitable for use in our model (Table S2).

3.2 | Similarity index

The difference between similarity indices calculated for 14 rivers, 28 years apart, is shown in Figure 2. Ayres and Clutton-Brock (1992) index of similarity ranged from 38% to 100% with our revised index of similarity ranging from 34% to 100%. Although the range of similarities between studies is comparable, our opposite riverbank similarity percentages are generally lower than those calculated by Ayres and Clutton-Brock (1992). The Jari is the only river that maintained the same percentage similarity from both studies, and the river with the largest disparity between the studies is the Juruá which now exhibits 35% less similarity than previously calculated.

3.3 | Multiple rivers: GLM

There was a highly significant negative relationship between mean streamflow (m^3/s) and the proportion of opposite-bank similarity (GLM, $N = 25$; $Z = -6.05$; $p \leq .001$; Figure 3). There was also a highly significant negative relationship between minimum streamflow (m^3/s) and the proportion of opposite-bank similarity (GLM, $N = 24$; $Z = -6.90$; $p \leq .01$; goodness of fit residual deviance/null deviance, 0.38). The association between width and the proportion of opposite-bank similarity was not

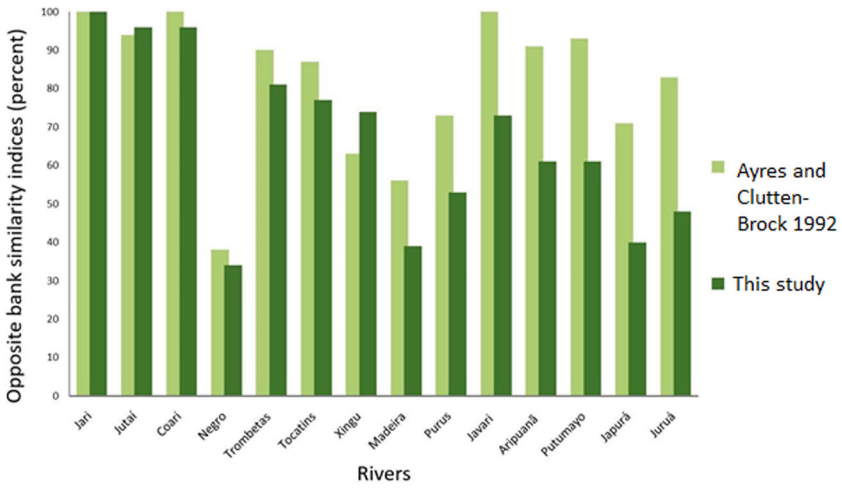

FIGURE 2 Comparison of similarity indices for opposite riverbank primate communities across 14 rivers in the Amazon watershed. Our analysis replicated the methodology of Ayres and Clutton-Brock (1992). Similarity was measured as (% species on side A common to side B) + (% species on side B common to side A)/2

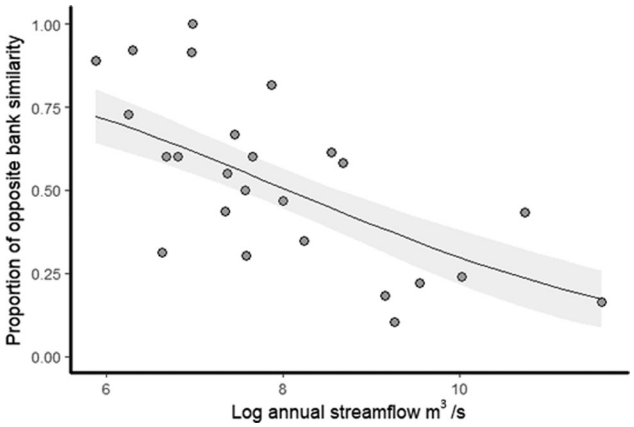

FIGURE 3 Logistic regression curve and 95% confidence limits for the effect of streamflow on the proportion of similarity between opposite riverbanks of 25 rivers in the Amazon basin

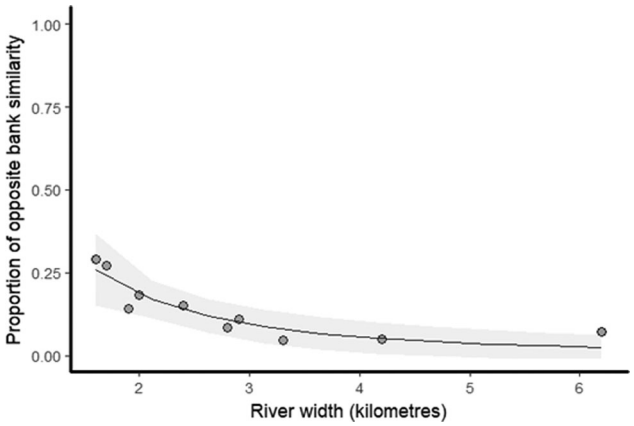

FIGURE 5 Logistic regression curve and 95% confidence limits for the effect of river width on the proportion of similarity between opposite riverbanks across ten 312-km segments of the Amazon River

significant (GLM, $N = 25$; $Z = 1.24$; $p = .21$; goodness of fit residual deviance/null deviance, 0.52).

3.4 | Amazon River: GLM

A significant negative relationship between mean streamflow and the proportion of opposite-bank similarity (Figure 4) was seen for the 10 Amazon River segments (GLM, $N = 10$; $Z = -3.03$; $p \leq .001$; goodness of fit residual deviance/null deviance, 0.12). A highly significant negative relationship between minimum streamflow (m^3/s) and the proportion of opposite-bank similarity across 10 Amazon River segments was also seen (GLM, $N = 10$; $Z = -3.05$; $p = .02$; goodness of fit residual deviance/null deviance, 1.02). There was a significant negative relationship between river width and the proportion of opposite-bank similarity across the 10 river segments (GLM, $N = 10$; $Z = -2.40$; $p = < .01$; goodness of fit residual deviance/null deviance, 0.52; Figure 5).

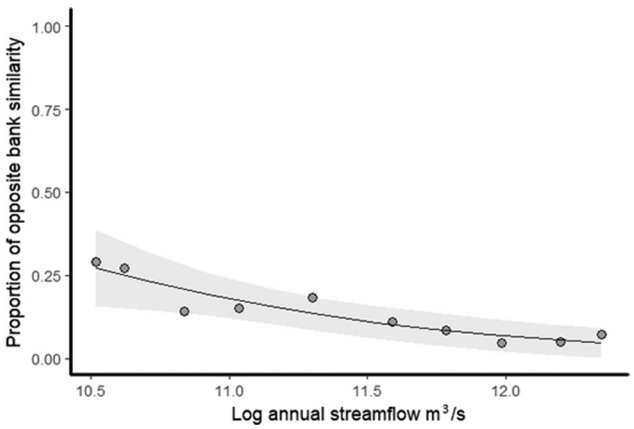

FIGURE 4 Logistic regression curve and 95% confidence limits for the effect of streamflow on the proportion of similarity between opposite riverbanks across ten 312-km segments of the Amazon River

3.5 | Influence of watershed: GLM

We found no significant difference in opposite-bank similarity between rivers grouped by distinct geological watershed (Guiana Shield; GLM, $N = 3$; $Z = 0.95$; $p > .05$; Brazilian Shield; GLM, $N = 3$; $Z = 0.47$; $p > .05$; Solimoes and Amazon basin; GLM, $N = 3$; $Z = 0.41$; $p > .05$, goodness of fit residual deviance/null deviance, 0.75).

4 | DISCUSSION

The controversy surrounding the extent to which rivers are drivers of platyrrhine speciation through vicariance is ongoing. Key issues include uncertainty over how to define species (Frankham et al., 2012; Groves, 2001a; Isaac & Purvis, 2004), species divergence estimates (Rull, 2008, 2011; Rylands et al., 2016) and river formation timing (Hoorn et al., 2010; Latrubesse et al., 2010). Research aiming to resolve platyrrhine phylogeny is ongoing (Hodgson et al., 2009; Osterholz, Walter, & Roos, 2009; Perelman et al., 2011; Ray et al., 2005; Schrago, 2007) and genetic and biogeographic investigations of the RBH have produced contrasting conclusions (Aleixo, 2004; Ayres & Clutton-Brock 1992; Boubli et al., 2015; Díaz-Muñoz, 2012; Gascon et al., 2000). In this study, based on the latest Neotropical primate species revisions and distribution data, we show a key prediction for the RBH still holds—that opposite-bank dissimilarity increases with increases in streamflow for multiple Amazonian rivers and for width for the Amazon itself.

The main mechanism underlying species richness and endemism in the Amazon basin is allopatric speciation. There are three principal ways in which rivers can function as landscape barriers and promote allopatric speciation (Ribas et al., 2012). First, evolution proceeds

along independent trajectories in distinct blocks due to river formation dissecting the landscape and dividing previously continuous populations, stranding primates on opposite riverbanks through vicariance. The RBH does not provide a strictly allopatric model because while genetic flow is hindered, there is no zero migration (Leite & Rogers, 2013). Second, rivers inhibit the dispersal of species from their centers of origin, causing them to be restricted to only one bank (Link et al., 2015). Finally, (compared with a landscape structure without barriers) when a species goes locally extinct on one riverbank, the probability of subsequent recolonization is lower. The role of the RBH in primate speciation through vicariance remains controversial and patterns should be broadly congruent between species with shared characteristics, that is, ecological requirements and vagility (Moritz et al., 2000; Rocha et al., 2015). Recent research on Amazonian drainage evolution shows the complexity of past geologic events, and there is ongoing controversy over the dating of river formation (Hoorn et al., 2010; Latrubesse et al., 2010). Underlying the RBH in the Neotropics is the assertion that the Amazonian river system formed before the speciation that produced extant species (Kay, 2015). Tectonic behavior of the Central Andes led to the evolution of the Amazon drainage basin. Based on geological evidence, Hoorn et al. (2010) placed the origin of major Amazonian rivers in the Miocene (~23.03–5.3 Ma), but others have determined younger dates, with differences between rivers (Latrubesse et al., 2010). These discrepancies have implications for the interpretation of historical diversification. Concordance between estimated divergence times for multiple species on opposite riverbanks in the Amazon can provide support to both river formation timing arguments and the RBH although uncertainties surrounding paleogeographic events, combined with a scarcity of rigorous tests for mechanisms promoting speciation, have led to a lack of consensus, with many studies finding little congruence between species, and few generalizations have emerged (Aleixo, 2004; Bates, Haffer, & Grismer, 2004; Boubli et al., 2015; Capparella, 1987; Díaz-Muñoz, 2012; Jacobs, Larson, & Cheverud, 1995; Leite & Rogers, 2013; Lynch Alfaro, Boubli, et al., 2015; Morales-Jimenez, Disotell, & Di Fiore, 2015; Moritz et al., 2000; Peres, Patton, Nazareth, & da Silva, 1996; Ribas et al., 2012; Rosenberger, 1992; Rull, 2008).

A key prediction of the RBH states that the strength of any river to act as a barrier is a function of its width and flow. Accordingly, similarity between opposite riverbanks should be greatest where the barrier effect is least, such as for smaller rivers, at river headwaters, or at the river mouth. Similarity analyses conducted on opposite-bank communities of birds concluded that rivers played a vital role in shaping present-day patterns of species composition (Hayes & Sewlal, 2004; Oliveira, Vasconcelos, & Santos, 2017). Alternatively, Gascon et al. (2000) performed the same analysis on frogs and small mammals between opposite banks of the Juruá river and found no evidence to support the RBH. The lack of congruent results between studies at different riverine locations can be attributed to variation in river dynamics, which have an important effect on the permeability of these barriers to dispersing organisms. For example, the apparent lack of a barrier effect from the Juruá in many studies can be explained by the fact that the barrier effect is not only related to streamflow and width, as we have tested in our analysis, but also the dynamics and underlying geological topography (Aleixo, 2004; Ribas et al., 2012). Shifting river courses may have resulted in occasional passive transfer of primates, and this lateral channel migration is much more common for rivers flowing through the Solimoes sedimentary basin than those running through the Brazilian and Guianan Shields. To explore how contrasting river dynamics might influence similarity, we compared rivers draining the three distinct watersheds. Comparatively, we expected to find average similarity higher in the Solimoes and Amazon basin, where rivers have a more unstable course; however, our results indicated no significant difference in similarity scores across the watersheds.

Between taxonomic groups, there is variation in sensitivity to vicariant mechanisms and this might explain contrasting diversification histories. Since the publication of Ayres and Clutton-Brock (1992) there have been significant methodological advancements in primate systematics. Taxonomic assessments were previously largely underpinned by the study of primate morphology. However, cytogenetic and molecular phylogenetic studies have provided increased detail on evolutionary relationships, often resulting in taxonomic revisions that increase species numbers (Link et al., 2015). Notably, in conjunction with advances in phylogenetics since the 1990s, there has been a shift in species concepts used in primatology. Testing hypotheses such as the RBH requires clear taxonomic and distributional species data, and similarity indices rest entirely on the notion of species. The established biological species concept has been criticized for the indeterminate status of allopatric species and an over-reliance on reproductive isolation to define species (Defler & Bueno, 2007; Frankham et al., 2012). The increasing adoption of PSC is implicated in rising species numbers (Groves, 2001a, 2004, 2013). The PSC is widely applied in most recent primate taxonomy research and provided the foundation for our database. Our data set included distribution information for primates at the species level which is a limitation, as more recently diverged lineages could provide a more detailed picture of biogeographic processes (Oliveira et al., 2017). However, subspecies delimitation is prone to a disagreement between authors and taxonomic assessments and as such, we did not see fit to include subspecies in our study. It is our view that including subspecies would further limit the strength of the analysis.

Our results, as compared with Ayres and Clutton-Brock (1992), illustrate how incorporating updated species information provides a check to conclusions generated in older studies. Using the latest classifications, the percentage of similarity in primate community composition for nearly every river analyzed is lower than similarity percentages based on older taxonomies. The Juruá river shows the largest discrepancy between the studies, with 35% less similarity than previously calculated. The evidence we present here corroborates the results of Ayres and Clutton-Brock (1992), but prompts the conclusion that they underestimated the effect of the RBH on Neotropical primates.

The distribution maps that we used from the IUCN Red List of Threatened Species Assessments 2008/2016 are based on either

observed occurrences or estimated ranges. Methods for estimating ranges, namely the extent of occurrence and the area of occupancy (AOO), can lead to bias (Burgman & Fox, 2003). Range data is limited and classifications, particularly those based on the AOO method, may be complicated by problems of spatial scale. However, there are correction techniques employed to minimize these and strict mapping standards applied by the IUCN (2013, 2019). Alternatively, distributions could have been obtained from the Global Biodiversity Information Facility (GBIF; Anderson et al., 2016). However, collections of occurrence data, such as the GBIF, suffer from biases, incompleteness, and taxonomic inaccuracies and therefore were not deemed adequate (Anderson et al., 2016).

Imprecision of mapped primate distributions in our model meant that some areas of estimated distribution overlap were considered unrepresentative of real-world primate ranges and were consequently disregarded. To avoid increased similarity, specifically across headwaters (due to increased permeability) from obscuring patterns of similarity more broadly, we discounted any distribution that crossed to the other side at the headwater only. Haffer (2008) criticizes authors invoking the RBH for overlooking problems associated with the lack of spatial separation of populations in headwater regions. Nonetheless, the scale is of critical importance and, where headwaters do allow localized gene flow, this does not prevent the application of the RBH for river sections further downstream.

Here, we report evidence to support a key prediction of the RBH, that similarity in the composition of opposite-bank communities should be highest where the barrier effect is lowest. Our analyses showed streamflow to be a highly significant predictor of opposite-bank similarity in primates. Congruent with Ayres and Clutton-Brock (1992), the results of our models demonstrate that rivers with higher streamflow act as more substantial barriers to dispersal, exhibiting greater variation in community composition. Because the Amazon River is so large and spatially configured with many tributaries, community composition was not the only variant between opposite banks but was also variable along the length of the river, which was not the case for most other rivers in the watershed. Segmentation captured this more complex arrangement of species distributions, enabling us to show that the barrier effect is not constant. Segments toward the river mouth which are wider and have greater streamflow exhibit less similar opposite-bank community composition than segments nearer the headwater. Our streamflow data were taken as the average of several monitoring stations per river and should, therefore, be more accurate than that used by Ayres and Clutton-Brock (1992). Notably, in their study, there was a secondary increase in similarity toward the mouth of the Amazon River. This pattern of similarity might be expected due to decreased water speed and associated sedimentation which creates islands that facilitate dispersal between opposite riverbanks. However, our model did not capture this as we did not extend our analysis that far through the delta due to a lack of streamflow data for that area.

Our results did not support a significant influence of width on similarity across the 25 rivers tested. This result contradicts our findings for the segmented Amazon River and is at odds with the findings of Ayres and Clutton-Brock (1992), and several studies of Amazonian bird composition (Hayes & Sewlal, 2004; Leite & Rogers, 2013; Oliveira et al., 2017). Some of the width data used in this analysis were obtained through measurement of satellite imagery, to provide mean estimates. This measure could be ineffective when attempting to identify predictors, as river width is highly variable. This limitation provides a possible explanation for the nonsignificant result and is supported by the finding of width as significant along the Amazon River, which used more robust width measures.

Due to significant variation in river characteristics and between taxonomic groups, it would be inappropriate to overgeneralize the barrier effect of rivers on community composition (Link et al., 2015; Lynch Alfaro, Boubli, et al., 2015). Mixed results demonstrate the extent of the complexities behind diversification. The capacity of a river to act as a barrier to species distributions and their capacity to prevent dispersal (Mitchell, Locatelli, Sesink Clee, Thomassen, & Gonder, 2015) is probably reduced when a meander loop is cut off or a new river course is carved out within the floodplain, transferring a portion of land to the opposite side of the river. Present understanding of this process is limited in terms of the extent of land that gets transferred or the frequency with which it happens (Haffer, 2008). We suggest that this process on geological timescales could allow even poorly dispersing primates to be passively transported across most small rivers and possibly large ones, convoluting RBH arguments or acting as a vicariance mechanism itself. Although beyond the scope of this study, further research should examine how the strength of a river to act as a barrier might be mediated by species-specific traits, such as the ability to colonize várzea forest and body size. Hayes and Sewlal (2004) provided evidence for the former, showing that the barrier effect was enhanced for birds restricted to terra firma and Ayres and Clutton-Brock (1992) found evidence for the latter by identifying a relationship between river size and the maximum size of species whose geographic range was restricted by the river. There are few studies testing the barrier effect specifically for floodplain specialists and the only research surveying floodplains over the entire length of the Amazon River (Cohn-Haft, Naka, & Fernandes, 2007) found considerable transitions in community composition in relation to the barrier effect of the river, despite continuity of the várzea.

Based on our results, rivers do broadly limit the distributions of Neotropical primates and appear to maintain diversity in the Amazon basin by isolating populations. We have provided evidence in support of the RBH, showing that river width and streamflow separating communities on opposite riverbanks can explain variation in composition. This was a broad-scale spatial analysis investigating patterns of community similarity within the context of riverine geography. Further phylogenetic research into the presence of reciprocal monophyly and sister taxa between riverbanks is required to determine whether rivers were the vicariant agent in the rapid diversification of Neotropical primates. Consideration of timing is the key to understand if rivers prompted allopatric speciation by dissecting previously continuous populations. Neotropical diversification is associated with complex

historical scenarios involving a range of spatial and temporal scales. Therefore, we argue that it is unlikely that any one theory can fully explain this diversity (Bush, 1994; Cortés-Ortiz et al., 2003; Rull, 2011). The vagaries of taxonomy make testing diversification theories challenging. We have demonstrated that results of older biogeographic studies should be viewed with caution, as incorporating the greater number of species now recognized can alter results. Accurate taxonomic and biogeographic information is essential for understanding the history of platyrrhine diversification and the processes that shaped their distributions.

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The authors confirm that this study complies with the legal and ethical requirements of the journal, participating institutions, and countries where research took place.

DATA AVAILABILITY STATEMENT

These data were derived from the following resources available in the public domain: The IUCN Red List of Threatened Species, https://www.iucnredlist.org/resources/files/bcfb6dac-60e6-4f0e-a027-02df540e512e; All The Worlds Primates, https://www.alltheworldsprimates.org/Home.aspx (subscription is free to range country primatologists); and the Global Runoff Data Centre https://www.bafg.de/GRDC/EN/01_GRDC/grdc_node.html.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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